

# Can Birds Smell?

A review of the literature on avian olfactory biology

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## **Abstract**

Research into avian olfactory biology and behaviour has been very limited up until the last 30 years. For a long time, it was thought that birds were anosmic or microsmatic, but in fact most birds have well-functioning olfactory anatomy that is strikingly similar to that of most other vertebrates. The use of olfaction varies considerably among bird orders and the sophistication of the olfactory anatomy is shown to be aligned with a species behaviour. Birds that have large olfactory bulbs and complex nasal structures are more likely to have a greater dependence on olfaction as a primary sense. However, even the presence of small or basic olfactory tissues enables a sense of smell and the modern belief is that probably all birds use olfaction in their everyday lives to some extent. The use of olfaction has been demonstrated to play a key role in some species for in species recognition, navigation, foraging and predator detection, reproduction and in one case, territorial defence.

## **Introduction**

Chemical cues are likely to have been the first cues ever used by organisms to assess their environment, (Caro, et. al, 2015) yet until recently ornithologists have had a hard time accepting that birds have a sense of smell (Birkhead, 2012). Part of this belief comes from birds beak being a hard structure that prevent the action of “sniffing” as seen in most mammals (Caro, et al., 2015) and partly from renowned ornithologist John James Audubon, who conducted a famous set of experiments in which demonstrated turkey vultures could not find carcasses that were hidden from sight (Audubon, 1831-9).

However, Audubon’s experiments were flawed as vultures prefer fresh carcasses whereas the experiment was performed with putrid meat (Birkhead, 2012). Despite this, the idea that birds could not smell persisted into the 20<sup>th</sup> century, when Alexander Hill “confirmed” this by killing a turkey after covering its food in sulfuric acid and potassium cyanide and concluded the turkey (and therefore all other birds) must not be able to smell (Hill, 1905).

It wasn’t until the 1960s that this view was seriously questioned again, when medical illustrator Betsy Bang noted the large, complex nasal cavities in multiple species of birds that she had dissected (Bang, 1960). Bang wondered why the nasal cavities varied so much among avian species, and her subsequent research changed the study of avian olfaction forever. More so, interest in avian olfaction has increased dramatically since the year 2000 (Caro, et al., 2015) but overall, to date there is still limited knowledge of olfaction in most bird species.

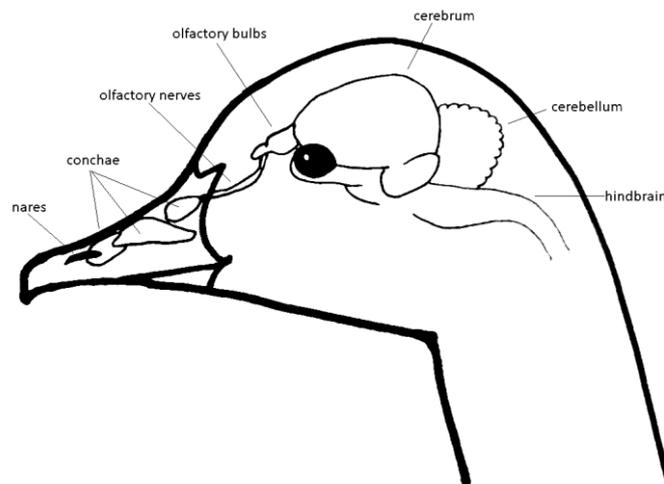
This review provides an overview of avian olfactory anatomy including comparison between species form and function. Researched examples of how birds utilise olfaction in their everyday lives (nominally for navigation, foraging, reproduction, recognition, predator detection and territorial defence) are also discussed.

## **Anatomical olfactory organisation**

Anatomical organisation of the olfactory system is similar in birds and other tetrapods (Caro, et al., 2015, Clark et. al., 2014, Roper, 1999). But unlike most other animals, birds have no vomeronasal organ or accessory olfactory bulb related to chemoreception (Roper, 1999 and Clark et. al, 2014). Since birds lack this mechanism for actively “sniffing” the air (with the exception of kiwi birds (Castro, et al., 2010)) – they most likely rely on inspiration or external movement of air to carry the chemical stimuli to the olfactory receptors (Roper, 1999).

The avian olfactory system consists of a pair of externa nostrils (nares), a series of nasal chambers (conchae) in the upper part of the beak, olfactory epithelial cells (in the third concha), olfactory nerves and the olfactory bulbs in the forebrain – Figure 1. Three nasal conchae are organised to warm, filter, moisten and chemically sample the inspired air (Caro, et. al., 2015, Bang 1960 and Clark, et. al., 2014). Inspired air passes through the nares into the first or second nasal chambers (or concae), where the incoming air is warmed and moistened (Roper, 1999). The first (anterior) concha is unique to birds and mostly serves as a thermoregulator. The middle (respiratory) concha contains mucus producing and ciliated cells (Bang, 1960). Some of the air is then passes from the second nasal concha into the buccal (or oral) cavity into the lungs, while the rest of the air is transferred to a third (posterior) concha containing the olfactory epithelium. These epithelial cells are mounted on invagilated cartilage (Roper, 1999). Each olfactory receptor cell has 6–15 cilia that extend into the cellular lumen (Shibuya and Tucker, 1967 in Clark, 2014).

The mucosa of the third concha is innervated by dense nerve fibres assembled to form the olfactory nerves that connect to the olfactory bulb in the forebrain (Caro, et al., 2015). The olfactory bulbs project to multiple brain areas that are homologous to areas that process olfactory information in mammals. (Caro, et al., 2015). Like other vertebrates, the olfactory bulbs of birds are bilaterally symmetrical, and each bulb is associated with the left or right brain hemisphere (Clark, et al., 2014)



*Figure 1; Basic anatomical structure of the avian olfactory system showing nares, nasal conchae, olfactory nerves and olfactory bulbs.*

### **Comparative form and function among species**

The complexity of olfactory anatomy varies considerably among bird species (Bang, 1960, Bang and Cobb, 1968, Birkhead, 2012). Elaborate olfactory systems are typically present in species that have a reliance on odour cues in the field (Clark, 2014). The size of the olfactory bulbs relative to the rest of the brain varies dramatically across avian orders from a ratio of over 25% in Cathartiformes (New World vultures) and Procellariiformes (petrels, albatrosses) to less than 5% in some Passeriformes (perching/ songbirds) (Bang & Cobb, 1968). More recent studies have shown the number of olfactory genes is correlated with olfactory bulb volume and is a better measure of olfactory importance (reviewed in Birkhead 2012).

A more complex or scrolled posterior concha correlates to a greater surface area and number of olfactory epithelium (scent-detecting cells) (Birkhead, 2012). The complexity of this concha also correlates with the relative size of the olfactory bulb (Bang and Cobb, 1968). For instance, this concha is heavily concaved in albatrosses and is scrolled 2.5 times in the turkey vulture (Bang, 1960).

The length of olfactory receptor cilia also varies by species. Black vultures *Coragyps atratus*, for example, have cilia of 40–50 µm, whereas domestic fowl have cilia of 7–10µm (Shibuya and Tucker, 1967 in Clark, 2014), which indicates greater sensitivity is associated with longer cilia.

Bang and Cobb's comparison of olfactory bulb size for 108 bird species concluded olfaction is of primary importance in kiwis, tube-nosed marine birds and vultures and is also likely to be useful in most other birds (Bang and Cobb, 1968). Kiwi behave very differently to most birds as they are ground living, nocturnal with poor eyesight (Castro, et. al., 2010, Taborsky and Taborsky, 2008). It therefore makes sense for them to primarily use senses other than vision in their everyday lives. Tube-nosed marine birds (order Procellariidae) include species of albatross and petrels. These birds travel over hundreds of kilometres of water during migration and mostly seek food from surface layers of the sea (Grubb, 1972 and Nevitt, 1999), thus navigation and finding food by scent is highly beneficial in this environment where visual cues are limited. New World Vultures (order Cathartidae) feed on carrion, spend a lot of time soaring at great heights (Grigg, et al., 2017) and relies on olfaction to scavenge in dense forests (Hopkins, 1888).

## **Influence and use of olfaction in avian behaviour**

### Individual and Species Recognition

In birds, the odours produced by the body mostly originate from uropygial secretions or feathers lipids. (Caro, et al., 2015). The chemicals of these gland secretions are species-specific (Jacob, et al., 1979). This may be important for species recognition in those similar species with that have spatial and temporal overlap, as mistakenly breeding with a different species may result in offspring that are nonviable, infertile or have reduced fitness.

Olfactory chemoreception is also likely to facilitate individual recognition among species. Pheromonal communications have been shown to play a role in the social behavior of domestic ducks (Jacob, et al., 1979) and Antarctic prions, *Pachyptila desolata*, have been shown to recognise their own and their partner's odour (Bonadonna, et al., 2007). Several species of petrels have been shown to be able to locate the entrance of their nesting burrow by smell (Caro, et al., 2015). These studies suggest personal odours may play a role in the olfactory signature of the individual and their nest.

### Navigation and Finding Food

Migrating seabirds are known to uses olfactory cues for foraging on ocean surfaces (Nevitt, 1999) and can also locate their remote island breeding colonies in a visually featureless seascape. This has been attributed to the birds being able to learn an olfactory map using wind-borne odors (Abolaffio, et al., 2018). Similarly, homing pigeons that have had their olfactory nerves sectioned became lost enroute (Papi et al., 1971 reviewed in Gagliardo, 2013). The so-called "olfactory navigation hypothesis" is pigeons in their home area learn windborne environmental odours in association with wind direction; and can determine the direction of displacement by recognition of local odours at the site of release and recall the direction these odours come from at the home area.

Other evidence of food-finding using olfaction has been documented in other birds including the (aforementioned) vulture (Grigg, et al., 2017 and Hopkins, 1888) and kiwi (Castro, et al., 2010 and Taborsky and Taborsky, 2008) but in different ways. Kiwis will actively "sniff" their food (Castro, et al., 2010) while turkey vultures will pass over carrion while gliding in thermal updrafts, but once the scent carried in the wind reaches them, will turn and follow the scent to the carcass (Hopkins, 1888). The importance of olfaction for foraging is also suggested among other bird species with small olfactory bulbs such as the domestic chicken (Jones & Roper, 1997), but in such cases is likely a secondary function to visual cues.

### Reproduction and Mate Choice

Olfactory signals have been demonstrated to reach brain areas controlling reproductive behaviours in birds (Caro, et. al. 2015) and these signals affect avian behaviour at all stages of reproduction, including

mate-choice and nest building. Individuals with the species dark-eyed junco, *Junco hyemalis* (a North American songbird) have been demonstrated greater reproductive success among males and females with volatile profiles that were more “male” or “female” like respectively (Whittaker, et al., 2013). Blue tits use certain species of plants within their nests to maintain an aromatic environment for nestlings (Petit, et al., 2002). This is most likely to aid in nest protection from parasites (reviewed in Scott-Baumann & Morgan, 2015)

#### Predator Detection and Territorial Defence

The use of olfaction to assess predation risk could be important in birds, particularly in habitats where visual detection of predators is impaired such as in nests or in dense forests. Blue tits will delay or refuse entering their nest if it has been spiked with a chemical smell of a known predator (Amo, et al., 2008). It has also been suggested that birds may be able to determine the diet of a potential predator to determine the level of threat (Amo, et al., 2014).

At least one case of the use of scent in defence of territory has been documented. Kiwi birds occupy large territories despite being unable to fly (Taborsky & Taborsky, 2008) and likely mark their territory using faecal scent marks (Castro, et al., 2010). However, this type of behaviour appears to be rare among birds.

#### Conclusion

The importance of olfaction has thus far been studied in a relatively small number of avian species, however the research to-date suggests vast possibilities within the remaining unstudied birds. Current research hints it is most likely that all birds use olfactory sense to some degree in their daily lives. With modern and emerging technology such as 3D brain imaging and genome sequencing increasingly available, it is likely that knowledge on olfaction in birds will only deepen in the coming years. Such discoveries may have the capacity to explain trends in phylogeny and avian life-histories.

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